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Characteristics and energetic strategies of the rhizosphere in ecosystems of the Bornhöved Lake district

O. Dilly [a,*], H.-J. Bach [b], F. Buscot [c], C. Eschenbach [a], W.L. Kutsch [a],
U. Middelhoff [a], K. Pritsch [b], J.C. Munch [b]

[a] *Ökologie-Zentrum, Universität Kiel, Schauenburgerstraße 112, D-24118 Kiel, Germany*
[b] *Institut für Bodenökologie, GSF — Forschungszentrum für Umwelt und Gesundheit, 85764 Neuherberg, Germany*
[c] *Lehrbereich Umwelt, Institut für Ökologie, Universität Jena, Dornburgerstraße 159, 07743 Jena, Germany*

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Abstract

This paper reviews investigations on interactions between soil microbiota, and plants during the interdisciplinary program ‘Ecosystem research in the Bornhöved Lake district’; it deals with processes associated with the rhizosphere at four agricultural, and forest ecosystems. Emphasis was placed on a black alder forest representing the interface between terrestrial and aquatic ecosystems. In the alder forest, more than 96% of the alder roots were colonised by ectomycorrhizal fungi. The diversity and vitality of these mycorrhizal rootlets exhibited local differences being generally lower at a dystric-dry site compared to an eutric-wet site close to the lake. Bacterial populations typical of well-aerated arable soils and rhizosphere soils were detected in samples taken from the soil at the eutric-wet site although unfavourable anoxic conditions were assumed to occur near to the lake. The composition of the bacterial populations seems to be profoundly influenced by the plant. Furthermore, the *Alnus–Frankia*-symbiosis showed a high spatial variability and was also more extensively established at the lake shore indicating both higher nitrogen requirement of the trees and higher energy supply for N_2-fixing actinomycetes by the tree. The high energy supply by the trees at the eutric-wet site could be confirmed by the soil carbon availability index. The role of plants on in situ soil respiration was estimated for agricultural and forest sites. The aggregated and modelled data for arable soil indicated that the respiration of roots and rhizosphere organisms contributed up to 40% of the total soil respiration during summer. An even higher contribution to soil respiration may have been derived from rhizomicrobial respiration in the alder forest. In conclusion, the amount of carbon delivered below ground seemed to be adjusted dependent on ecosystem type and environmental conditions. In particular, alder trees seemed to have established a beneficial environment for the microbiota in the rhizosphere. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Alder; Beech; Maize; Microbial eco-physiology; Soil respiration; Root growth

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1. Introduction

The research program ‘Ecosystem research in the Bornhöved Lake district’ is one of five German ecosystem-related projects with the objective of interdisciplinary analyses and modelling of structures, dynamics and functions of terrestrial and aquatic

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* Corresponding author. Tel.: +49-431-880-4085;
fax: +49-431-880-4083.
E-mail address: oliver@pz-oekosys.uni-kiel.de (O. Dilly)

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ecosystems. The core program started in 1988 and will be completed in 1999. The principal scope is intended to continue at the Ecology-Centre that has been founded in 1996.

The rhizosphere is known as the zone of greatest interrelationship between plants and microorganisms and has the highest activity of the soil microbiota (Grayston et al., 1996). The majority of plants are mycorrhizal which apparently shows the substantial interdependence of plants and microorganisms. Symbiosis and association of plants with microorganisms such as mycorrhizal fungi and N_2-fixing bacteria may improve nutritional status of both plants and soil microbiota. The free-living heterotrophic microbiota in the rhizosphere and soil disconnected to the root are favoured by the nutrients that are derived from exudates of plant roots. These readily available substrates are considered as the factor most limiting microbial growth in soil (Wardle, 1992). This confirms the view that this ‘beneficial biotope’ is of crucial importance for the functioning of terrestrial ecosystems.

Investigations related to the interactions between plant and soil microbiota and, thus, the biological functioning of the rhizosphere have been carried out multidisciplinarily in agricultural and forest ecosystems. The main interest was focussed on a black alder forest representing the interface between terrestrial and aquatic ecosystems. The manifold approaches enabled the combination of data from different levels and the calculation of balances to evaluate the interdependence of plants and soil microorganisms. This review interrelates results from this program that contributes to the knowledge about the rhizosphere. We focussed on (i) the structural composition of soil microbiota in a black alder (*Alnus glutinosa* (L.) Gaertn.) forest with reference to mycorrhiza and composition of the bacterial communities in the bulk soil; (ii) activity of the microbiota concerning N_2-fixation and also soil respiration measurements in forest and agricultural systems; (iii) carbon balances at the system level leading to the ecosystem-related energetical view on the rhizosphere.

2. Site description

The research site is located some 30 km south of Kiel in Schleswig–Holstein, northern Germany (54°06′N, 10°14′E) in a landscape formed during the *Pleistocene* (“Ostholsteinisches Hügelland”) with a climate influenced by the North Sea and the Baltic Sea. Long term (1951–1980) mean annual precipitation was 697 mm and average annual air temperature was 8.1°C.

The main terrestrial research area comprised two soil catenas, one under agricultural use and one consisting of different forests (Fig. 1). The soils of the sites (Table 1) were predominantly sandy and have varying contents of organic matter and pH values. The agricultural catena included a field with maize (*Zea mays* L.) monoculture, regularly fertilised with inorganic fertilisers and cattle slurry, irregularly with organic manure. The forest sites included a beech (*Fagus sylvatica* L.) forest and two sites in a black alder (*A. glutinosa* (L.) Gaertn.) forest. One site was located adjacent to the lake Belau and another approximately 50 m away inside the forest at the foot of a hill. The soil reaction of these two topsoils (horizon below litter) differed substantially (Table 1) and the sites were therefore called the eutric-wet and the dystric-dry alder forests. The alder forest soils were seasonally poorly drained and waterlogged.

3. Structure of the microbiota

3.1. Composition of the mycorrhizal communities in the black alder forest

The mycorrhizal community of the alder forest consisted of 16 different ectomycorrhizal types that have been identified using morphological characterisation and molecular tools (Pritsch et al., 1997). The composition of the ectomycorrhizal community based on morphological determinations differed between the eutric-wet and the dystric-dry sites (Fig. 2). The latter is characterised by the lack of *Lactarius* and *Cortinarius*-type mycorrhizas, which were abundant at the eutric-wet site. *Cortinarius* spp. have been present only at the eutric-wet site and exhibited an extensive extramatrical mycelium (Fig. 3).

3.2. Composition of the bacterial communities in the black alder forest

The bacterial communities have only been investigated at the eutric-wet site (Bach, 1996). *Pseudo-*

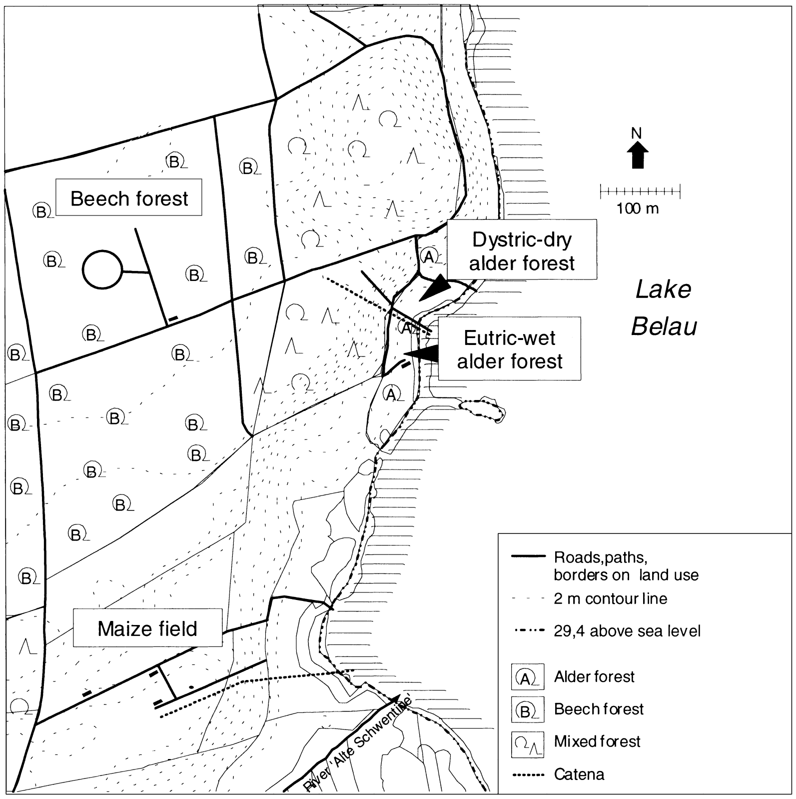

Fig. 1. Geographical location of the sites considered in the principal research region in the Bornhöved Lake district.

monas, *Flavobacterium-Cytophaga*, *Alcaligenes*, *Arthrobacter* and *Promicromonospora* were found to be the predominant heterotrophic bacteria. *Pseudomonas fluorescens* biotypes, *Bacillus cereus* and *Bacillus mycoides* and *Flavobacterium-Cytophaga* were identified to be the main proteolytic bacteria (Bach and Munch, 1999). *Cellulomonas*, *Pseudomonas* and *Bacillus* were determined as the most abundant cellulolytic bacteria. For the isolation of these bacteria, media with low substrate concentrations and pH values corresponding to those in the soils, incubation temperature of approximately 12°C which was the field temperature at the sampling date and long-term incubation were applied to reduce laboratory selection of

Table 1
Properties of soils in the landscape of Northern Germany

	Horizon	Depth (cm)	pH ($CaCl_2$)[a]	C_{org} (mg g^{-1} soil)[b]	C/N (w w^{-1})[b]	Bulk density (Mg m^{-3})[c]	Soil type FAO (1988)
Maize field	Ap	0–20	4.6	11.9	10	1.3	Dystri-cambic Arenosol
Beech forest	Ah	0–5	3.3	29.2	15	1.1	Dystri-cambic Arenosol
Dystric-dry alder forest	H	0–20	3.8	328.4	15	0.2	Dystric Histosol
Eutric-wet alder forest	H	0–20	5.8	262.1	17	0.2	Eutric Histosol

[a] In a suspension of fresh soil: 0.01 M $CaCl_2$=1:4 (w v^{-1}).
[b] Determined in air dried soil samples using CHN–O Rapid Analyser (Heraeus, Hanau).
[c] Estimated in soil cylinders of 5.8 cm in diameter and 4 cm in height that were dried at 105°C until mass equilibrium.

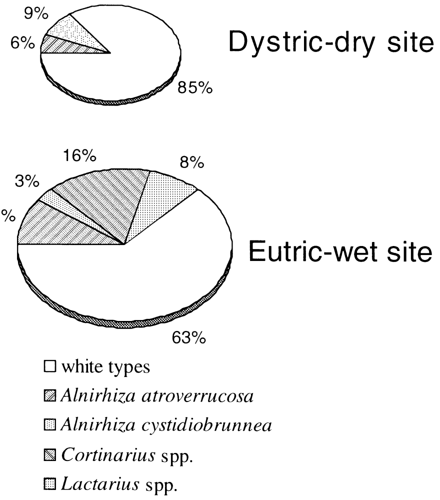

Fig. 2. Composition of the mycorrhizal community at two sites of an alder forest (after Pritsch, 1996); summarised frequency of 12 samplings between May 1993 and August 1994; the size of the pies represents the relative total length of mycorrhizal roots.

fast growing organisms. The experiments were done for three samplings in spring 1992 and spring and autumn 1993 at least in triplicate for each date. Whereas predominantly K-strategists were cultivated by this procedure from an adjacent grassland soil (Bach, 1996), organisms that can be regarded as r-selected bacteria and typical for the rhizosphere were found in the alder forest soil. This was surprising because they were isolated from soil samples that were not specifically taken from the rhizosphere. Furthermore, the isolated culturable communities were similar in terms of numbers and predominant species within the physiological groups to those in aerated sandy agricultural soils of the Bornhöved Lake district. Although the alder forest soils were regularly flooded by lake water, facultative anaerobic bacteria were much less frequent in the adjacent, seasonally flooded grassland (Bach, 1996). High in situ soil respiration at the eutric-wet site (Dilly et al., 1999) suggests that available organic matter is continuously oxidised, at least in the upper soil horizons. The bacterial populations in the alder forest soils seemed to be adapted to the degradation of readily available C compounds. This suggests that the alder trees at the eutric-wet site have had a substantial impact on the whole soil comprising both rhizosphere and soil away from roots. The alder trees seemed to ascertain sufficient readily available carbon compounds and oxygen level in the soil. The second may be attributed to their ability to actively transport oxygen to the roots as reported by Grosse and Schroeder (1984). However, the oxygen supply to the soil by the root is not assured (Wötzel, 1997).

3.3. Composition and the strategy of the soil microbiota

We applied several methods to estimate the microbial biomass content in soils. All methods have advantages, drawbacks and limitations (Martens, 1995). It is, however, more and more accepted that each method refers to another subset of the microbial biomass (Wardle and Ghani, 1995). Therefore, the combination of complementary methods may provide adequate information about the structure of microbial communities. The metabolic-responsive microbiota determined by

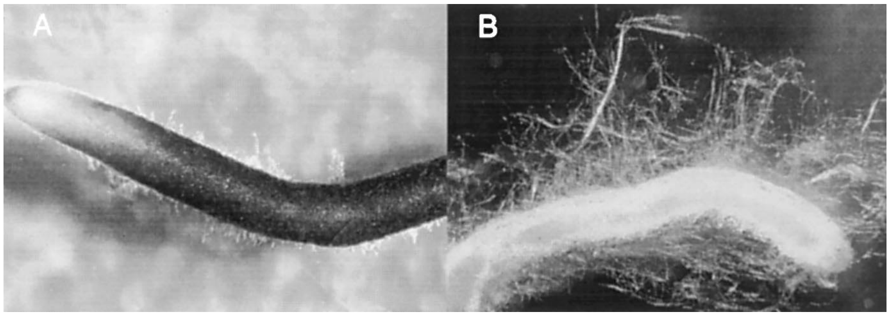

Fig. 3. *Alnirhiza cystidiobrunnea* (A) and *Cortinarius* mycorrhiza (B) on black alder; *Cortinarius* was only present at the wet site of the alder forest (after Pritsch, 1996).

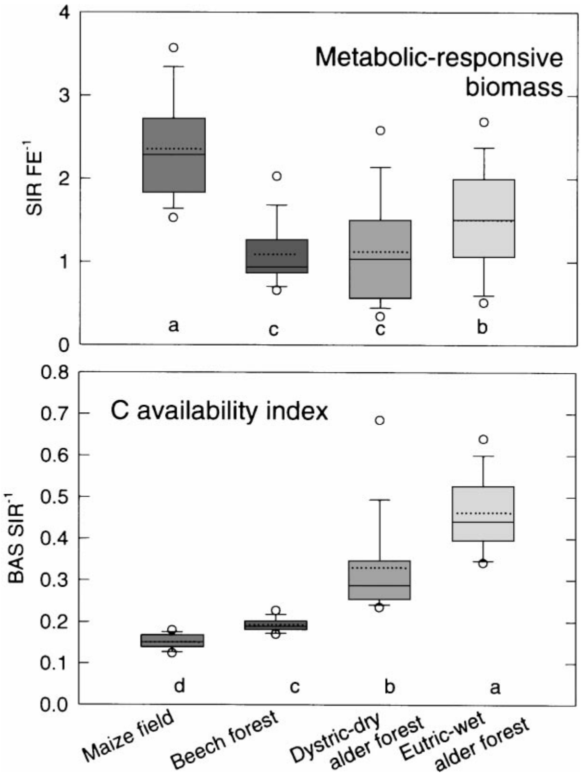

Fig. 4. Metabolic-responsive microbial biomass, indicated by the quotient between substrate-induced respiration and fumigation–extraction obtained biomass values, and carbon availability index, indicated by the quotient of respiration rate without and with glucose addition, in topsoils of maize field, beech forest, dystric-dry and eutric-wet alder forest in the Bornhöved Lake district (data from 1992, n=12; different letters indicate significant differences when applying the Mann–Whitney rank sum test, $p<0.05$; boxes encompass 25 and 75% quartiles, the central and the broken lines represent the median and the mean, respectively, bars extend to the 90% confidence limits and circles show data outside the 10th and 90th percentiles).

the quotient of substrate-induced respiration and the fumigation–extraction significantly differed between the topsoils of the arable maize-monoculture field, the beech forest, the dystric-dry site and eutric-wet alder forest (Fig. 4). The first method refers to organisms that can be activated by substrate (glucose) addition and the second to both activated and resting, fumigation-sensitive organisms (Dilly and Munch, 1998). Thus, the highest metabolic-responsive microbiota in the topsoil are present in the field and decreased in the order, eutric-wet alder forest > beech and dystric-dry alder forest. The high values in the soil of the eutric-wet site suggest also the dominance of r-strategists (Dilly and Munch, 1998), which concurs with the composition of the bacterial communities (Section 3.2).

The differences between the dystric-dry and eutric-wet sites may be explained by the carbon availability index as proposed by Cheng et al. (1996) which relates the respiration rate without, BAS, and with addition, SIR, of sufficient readily available substrate. Readily available C substrates that are frequently limiting microbial growth in soil (Wardle, 1992) were found to be generally higher at the eutric-wet than at the dystric-dry site which may explain the variation of the activity status of the microbial biomass. The beneficial effects of the plant were apparent particularly at the eutric-wet site, which concurs with the structure of the soil bacterial community discussed above. In the topsoil of the maize-monoculture field, the highly active microbial biomass seemed to deplete the available resources regularly and, consequently, to starve. In summary, fair amounts of readily available C substrates seemed to be present particularly in the eutric-wet alder forest soil.

4. Activity of the microbiota

4.1. N_2-fixation by the Alnus–Frankia-symbiosis

The development of the symbiosis between alder and *Frankia* showed a high spatial variability inside the forest (Dittert, 1992; Dilly et al., 1999). All together, the symbiosis was established more extensively at the lake shore. In the alder forest, symbiosis between alder and *Frankia* appeared to fix about 40–45 and 70–85 kg N ha^{-1} a^{-1} at the dystric-dry and eutric-wet site, respectively (Dittert, 1992). The data originated from at least monthly determinations in 1989 and 1990 and represent the lowest range because calculations were based only on leaf and stem growth; the root system, organs for reproductions and twigs were not considered. When assuming carbon costs of 10 g C g^{-1} N fixed, which fits in the range as reported by Marschner (1995), this corresponded to an energy demand of 0.04–0.08 kg C m^{-2} a^{-1} at the dystric-dry and eutric-wet sites, respectively. Because the N_2-fixation mainly occurred during the assimilation time from spring to autumn, these amounts are equivalent to approximately 8 and 6% of the in situ CO_2-C emissions at the dystric-dry and eutric-wet sites, respectively, as calculated by Dilly et al. (1999). Thus, the N_2-fixation process consumed a considerable amount of the energy transferred into below ground at the two sites of the alder forest.

4.2. Soil respiration

Soil respiration measured under field conditions combines the respiration of roots and rhizosphere microorganisms (rhizomicrobial respiration) and also the respiration of the humus-degrading organisms present in the bulk soil. Activity of soil fauna generally contributes, to a minor extent, to soil respiration (Yanagita, 1990).

Fig. 5 shows the annual courses of soil respiration in the maize field, the beech forest and the alder forest in 1992 and 1993 from summarised data on carbon fluxes provided by Kutsch et al. (2000). The values for the maize field and the beech forest were extrapolated by models of decomposition of fresh and older organic matter (Kutsch and Kappen, 1997) and of rhizomicrobial respiration dependent on root biomass and soil temperature for three classes of roots in the beech forest and one in the maize field. Root biomass and soil respiration rate varied throughout the growing season according to the aboveground development for maize (Kutsch, 1996) but not for beech. The rhizomicrobial sub-model of beech was calibrated by data from Kakubari (1988) and Gansert (1994). The alder forest values were simply estimated by means of a temperature correlation according to Eschenbach et al. (1997). All models were validated by field measurements of soil respiration (Kutsch, 1996; Eschenbach et al., 1997; Kutsch, unpublished data).

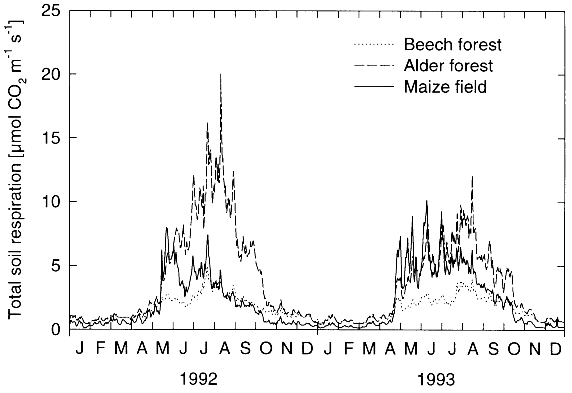

Fig. 5. Modelled annual courses of total soil respiration for the alder forest, the beech forest and the crop field in 1992 and 1993.

In 1992 and 1993, total soil respiration was the highest in the alder forest and the lowest in the beech forest. This high rate in the alder forest can be explained by a strong mineralisation of litter, root respiration and respiration of mycorrhiza, *Frankia*-nodules, free-living rhizosphere and bulk soil organisms which all acquire assimilates from the roots. Calculations of Dilly et al. (1999) showed that 80 and 86% of the in situ CO_2-C were attributed to both rhizomicrobial respiration and soil organic matter degradation at the dystric-dry and eutric-wet site, respectively. Approximately 20 and 14% were attributed to the rapid degradation of the fresh litter. Assuming that the soil humus contributes to the same C amounts as fresh litter, 60 and 73% of the in situ CO_2-C was derived from rhizomicrobial respiration. This refers to 0.5–0.8 mm lowering of the soil surface for the given bulk density of about 0.2 Tg m^{-3} (Table 1). At the two sites of the alder forest, most C of the soil respiration appears to come from the rhizosphere.

Soil respiration measurements at the maize field during the growing season in 1992 (Kutsch, 1996) were conducted to estimate the proportion of rhizomicrobial respiration in this system (Fig. 6). The considered data for soil respiration were determined

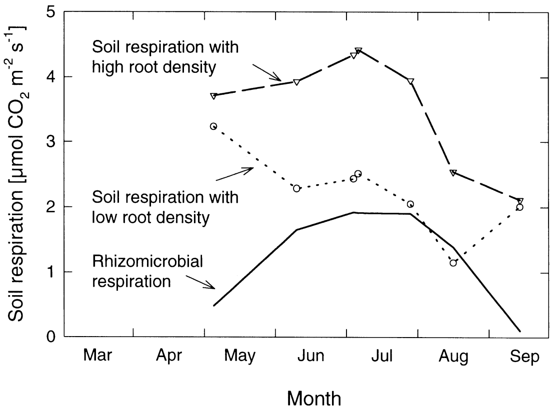

Fig. 6. Effect of root density on soil respiration of the maize field in 1992; each symbol reflects the mean activity rate at 18°C for the respective date (after Kutsch, 1996).

during numerous days using three cuvettes. Since no vegetation has been grown in spring, all respired C could be attributed to the respiration of the bulk soil microorganisms. During the growing season, maize roots intensively colonised the soil to exploit nutrients. Comparative measurements between sites close to the plants with high root density and those more distant with low root density (Fig. 5) indicate that up to 40% of the soil respiration was attributed to the plant roots and the rhizosphere during this summer. During spring 1993 the maize field received large amounts of organic manure. This fact together with high temperatures in the not-shaded soil explained the total soil respiration being similar in maize field and the alder forest in spring and early summer 1993. However, most of the CO_2 emission has been derived from the decomposition of organic matter in the maize field.

Concerning the methodology, it seems almost impracticable to precisely estimate the relative contribution of the different components to the total soil respiration rates. The use of labelled compounds is rather expensive and appropriate labelling of all relevant soil pools are presently unrealisable. Since we did not use labelled compounds in our approaches, we calculated balances using the broad spectrum of accessible data. We think that the calculation of balances and the comparison of adjacent sites with high and low root densities gave a reliable estimate and should generally be considered to calculate the relative contributions from rhizosphere systems to the total respiration rates.

5. Energetic efficiency of the ecosystems

Table 2 shows the calculated carbon balances of ecosystems in the Bornhöved Lake district in 1992 by using a bottom-up modelling approach (after Kutsch et al., 2000). Four sub-models were combined to calculate ecosystem net CO_2-fluxes considering measured microclimate data and on an hourly basis: (i) a canopy gas exchange model, (ii) an aboveground plant respiration model, (iii) a model of decomposition in the bulk soil, and (iv) the model of rhizomicrobial respiration (see Section 4.2). Each model was carefully calibrated by field data. When data were not available for model calibration in 1992, we considered measurements from other years and comparable studies (Möller et al., 1954; Penning de Fries et al., 1987; Kakubari, 1988; Klepper, 1991; Schulte, 1993; Gansert, 1994; Steinborn et al., 1998). To ascertain the balances, we now apply eddy-covariance method in the beech forest as described for instance by Valentini et al. (1996).

Table 2
Carbon fluxes in ecosystems in the Bornhöved Lake district (after Kutsch et al., 2000)

	Alder forest	Beech forest	Maize field
(a) Gross primary production[a]	2280	1084	1677
(b) Rhizomicrobial respiration	−1295	−243	−266
(a)–(b) Carbon for plant growth	985	841	1411
(c) Total soil respiration	−1570	−634	−718

[a] In g C m^{-2} a^{-1} for the year 1992.

Gross primary production and rhizomicrobial respiration was apparently the highest in the alder forest and the lowest in the beech forest. Alder trees here exhibited a low leaf area index and produced new leaves continuously in the periphery while starting with litter fall from the inner parts of the crown in summer (Eschenbach and Kappen, 1996). The heliophil leaves were uniformly distributed in the canopy, showed no differentiation in sun and shade leaves but a high maximum net photosynthesis rate throughout the complete canopy (Eschenbach, 1996, 2000). In contrast, the net primary production was the highest in the maize field and the lowest in the beech forest. High C assimilation rates via photosynthesis and high C liberation rates via the roots classify *Alnus* as r-strategist in the sense of Andrews (1991). The high amounts of C allocation below ground suggest a high energy requirement to overcome low nutrient availability.

Table 3 shows the energetic efficiency at a dystric-dry and eutric-wet site of the alder forest. Stem production was slightly higher with younger trees at the eutric-wet site but ranged in the same productivity class at the two sites according to Schober (1987). The below ground characteristics: (i) mean fine root biomass, (ii) fine root growth, (iii) abundance of root nodules, and also (iv) soil respiration were significantly higher at the eutric-wet site. Studies on mycorrhizal rootlets generally revealed lower vitality at the dystric-dry site and a considerably lower potential for regeneration than at the eutric-wet site close to the lake. The total vital mycorrhizal rootlets were 4.5 and 11.2% at the dystric-dry and the eutric-wet sites,

Table 3
Characteristics and energy budget at two sites in the alder forest after Middelhoff (2000, modified)

	Dry site	Wet site
Above ground		
Tree age (a)	66	45
Basal area of the trunks (cm^2 m^{-2})	53	50
Stem biomass (kg dry mass m^{-2})[a]	23.2	15.7
Productivity (kg dry mass m^{-2})[b]	0.35	0.45
Surface of tree crowns per area (m^2 m^{-2})[c]	1.71	3.25
Below ground		
Alder fine root biomass (kg dry mass m^{-2})[a]	0.11	0.33
Alder fine root biomass production (kg dry mass m^{-2} a^{-1})[a]	0.32	0.66
Area density of *Alnus–Frankia* root nodules (cm^3 active tissue m^{-2})[d]	74	260
Soil respiration (kg C m^{-2})[e]	0.5	1.4

[a] In 1992; ash-free dry mass at 70°C, stem biomass calculations based on determinations of BHD (stem diameter at 120 cm above ground) and heights of trees, production based on coring measurements. Fine root production referring to the difference between minimum and maximum biomass from results of sequential coring.

[b] In 1992; corresponding to the same classification of site quality ‘I, 5’ at the two sites after Schober (1987).

[c] GIS-aided calculation based on a single tree map and tree heights for 1992.

[d] In 1989 and 1990 after Dittert (1992).

[e] For the 1992 growing season, adopted from Dilly et al. (1999).

respectively (Pritsch, 1996). This was particularly evident in the phase of rapid root growth in spring during which the total length of mycorrhizal roots was estimated to be threefold longer at the eutric-wet site compared to the dystric-dry site (Fig. 2).

These effects were attributed to the higher assimilation capacity by the expanded crown surface which was permitted by the edge position. The nutritional conditions do not seem to allow extended stem growth at the eutric-wet site in comparison to the dystric-dry site. High leaf area index leads to high assimilation rates and profound circulation of nutrients in the litter. Elevated net C assimilation at the eutric-wet site seemed to trigger either N_2-fixation rate enabling the growth of N-rich leaves or the growth of root and mycorrhiza. The alder trees appear to allocate extensively carbon to the roots acclimating the high C gain and restricting nutrient availability (Middelhoff, 2000).

A. glutinosa seems to provide large amounts of energy to the symbiosis with *Frankia*, to the mycorrhizae, and to the rhizosphere. Root exudates are known to enable the mobilisation of phosphorus (Bar-Josef, 1991), whereas *Frankia*-symbionts provided nitrogen to the tree (Dittert, 1992), and mycorrhizae are regarded as being beneficial in terms of mineral nutrients uptake and transfer to the plant (Read, 1992). The ratio of net primary production to rhizomicrobial respiration suggests that the strategy of alder under the environmental conditions is to be inefficient with reference to C use in comparison to beech and maize. However, energy supplied to the rhizosphere may support the growth of microorganisms, i.e. mycorrhizal mycelium, which enables the alder trees to utilise physically limited nutrient resources in soil. In addition, microorganisms can use this energy for producing large amounts of extracellular enzymes. High biomass-specific protease activity rates were estimated for the eutric-wet site of the alder forest (Dilly and Nannipieri, 1998). Furthermore, phosphatase activity rates were additionally high in the alder forest (Dilly, 1999), which may contribute to high cycling rates of low P pools in the Histosols of the alder forest as reported by Wachendorf (1996). The ecophysiological characteristic with regard to C use proposes a certain degree of profit of the plants. According to the teleological rationale, we can conclude that the alder plants spent substantial parts of their assimilated energy to adjust to the environment conditions probably mainly in order to establish the most appropriate beneficial rhizosphere.

In well-drained soils of the Bornhöved Lake district, the availability of P and probably also N is higher and, therefore, *F. sylvatica* and *Z. mays* need less C resources to invest in the root system and the mycorrhiza. The maize field is controlled by the management of the farmer with the aim of high yield. The fertiliser ensures low energy losses for nutrient uptake and high net primary production. *A. glutinosa* is a typical pioneer tree (Eschenbach, 1996) exhibiting a system with high internal flux rates but low efficiency, whereas *F. sylvatica* being a late successional tree species provides low internal flux rates with high efficiency.

6. Conclusions

Although we could only analyse a minute part of the aspects relevant to the rhizosphere in the interdisciplinary program 'Ecosystem Research in the Bornhöved Lake district' several structural and functional conclusions concerning rhizosphere functioning for agricultural and forest ecosystems could be deduced:

- High diversity and vitality of mycorrhizal rootlets seemed to occur under favouring microenvironments being supplied by the plant particularly at the eutric-wet site of the alder forest.
- Bacteria adapted to high oxygen levels and typical for the rhizosphere were present in soil of the eutric-wet site of the alder forest even at times when soil water was in excess.
- Activity measurements indicate that a substantial amount of energy from the plant was transferred to the symbionts and other beneficial organisms particularly apparent at the eutric-wet site of the alder forest.
- Regarding the energy transfer at the system level, interactions between plants and microorganisms seem to be of great importance for elemental transfer towards the plant and the soil. These interactions seriously control soil characteristics.

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